

# Comments

*Ecology*, 85(4), 2004, pp. 1160–1165  
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## DO ALTERNATE STABLE COMMUNITY STATES EXIST IN THE GULF OF MAINE ROCKY INTERTIDAL ZONE? COMMENT

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Petraitis and Latham (1999) hypothesized that rockweed stands and barnacle–mussel beds on sheltered rocky shores in New England may represent alternative states and outlined experimental tests suitable to address this question. They advanced this hypothesis because mussels and the seaweed *Ascophyllum nodosum* are often codominant in sheltered bays (Lewis 1964), and their co-occurrence is not adequately explained by the standard paradigm of consumer control (Menge 1976, Lubchenco and Menge 1978). Petraitis and Latham (1999) also suggested that the development of alternative states depends upon the timing and spatial scale of pulse perturbations. In Petraitis and Dudgeon (1999) and Dudgeon and Petraitis (2001), we reported the results of experiments that show patch size determines the rates of predation and recruitment. Our results provide evidence consistent with the formation of alternative communities on rocky shores of sheltered bays.

Bertness et al. (2002) extended and tested our hypothesis about alternative states to other intertidal habitats in New England. They concluded that rockweed stands and barnacle–mussel beds are highly deterministic systems driven by the interaction of water flow, larval input, and consumer pressure. They suggested the type of habitat in which mussels and seaweeds exist as alternative states is likely to be rare. We are delighted that Bertness et al. have conducted experiments to test if mussel beds and rockweed stands are alternative states. We agree that it is crucial to duplicate experiments so that ecologists can move beyond debates of

“different ecologies or different ecologists” (Underwood and Fairweather 1986). We applaud such efforts.

Our applause, however, is muted because Bertness et al.’s (2002) experiments do not replicate our design as claimed and fall short of being valid tests of alternative stable states. We first compare their design with our design because the problems with their study as a test of alternative stable states arise from the design itself. We then discuss the criteria outlined by Petraitis and Latham (1999) for testing the hypothesis of alternative stable states and the limitations of Bertness et al.’s design as a test of the hypothesis. We also have concerns that their experiment has more general problems of experimental design and analysis. We are well aware that undertaking a critical review has inherent risks (Leeper 1948, Hurlbert 1984) but we hope our reply will help highlight not only the difficulties of testing for alternative states in natural systems but also common pitfalls of experimental design and analysis.

### *Differences in designs*

Our design had five levels of patch size (circular clearings of 1-, 2-, 4- and 8-m diameter and an uncleared control) crossed with 12 sites. All 12 sites were on sheltered shores and in large, well-established *Ascophyllum* stands. The sites were structured so that three sites were nested within each of the four bays on Swan’s Island, Maine, USA (see Dudgeon and Petraitis [2001; Fig. 2] for a map of sites). Clearing sizes were considered a fixed effect, and bays, sites nested within bays, and interactions were considered random effects

Bertness et al. (2002: 3437) stated that “we replicated Petraitis and Dudgeon’s (1999) experiment”. They did not. They established three treatment levels for the effect of patch size. The treatment levels were square clearings of 1 × 1 m and 3 × 3 m plus an uncleared control. Within each patch type, they placed three caging treatments: a 20 × 20-cm exclusion cage, a 20 × 20-cm cage control, and a 20 × 20-cm uncaged control. The set of nine treatment combinations was established at eight *Ascophyllum* sites and eight mussel sites along a 10-km stretch of the Damariscotta River estuary in central Maine. The *Ascophyllum* and mussel sites differed in the amount of water flow. The *Ascophyllum* and mussel sites also appear to have been paired since the *Ascophyllum* sites were described as adjacent to the mussel sites. Bertness et al. reported that one mussel site was lost during the first winter due to ice scour. All three factors (habitat type, patch size, and caging) and all interactions were considered fixed effects. The pairing of sites, which would be a random block effect, was ignored.

Manuscript received 31 March 2003; revised 16 August 2003; accepted 23 August 2003. Corresponding Editor: S. G. Morgan.

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*The criteria for testing alternative stable states*

Bertness et al. (2002) have glossed over several important aspects of testing alternative stable states, and thus their experiment does not meet the basic criteria needed to conduct a valid test. There are four critical requirements. First, the physical environment must be initially the same at all sites in which the test is done (Connell and Sousa 1983, Peterson 1984, Sousa and Connell 1985). Second, the initiation of alternative states may require large disturbances, and so the size of the disturbance event should be experimentally manipulated over a large range of spatial scales (Knowlton 1992, Petraitis and Latham 1999). Third, the perturbation that initiates the change in state must be a “pulse” event, and the formation of different communities cannot be caused or maintained by “press” effects (Connell and Sousa 1983, Peterson 1984). Finally, the experiment must be carried out over a sufficient time period to ensure that the alternative states are self-sustaining (Connell and Sousa 1983, Peterson 1984).

The first three criteria address the experimental conditions for a valid test, and the fourth criterion addresses community persistence (Drake 1991, Petraitis and Latham 1999). Experimental tests of alternative states—stable or not—only require showing that pulse events can initiate the “switch” (sensu Wilson and Agnew 1992) between different assemblages. Petraitis and Latham (1999) distinguished tests of the initiation of alternative states from tests of maintenance. Tests of maintenance are more difficult and require proving an established assemblage is self-replicating. We have focused on the initiation of alternative states in *Ascophyllum* stands because of the difficulties in testing stability per se. We have been very careful to use phrases such as “alternative states” rather than the more familiar phrase, “alternative stable states” throughout our presentations of the experimental work.

Bertness et al. (2002: 3436) stated that their experiment is “designed to examine the hypothesis that mussel beds and *Ascophyllum* canopies can be alternative community stable states on rocky shores in the Gulf of Maine,” but the experiment fails to meet all four requirements. They used two different environments, and we think their patch clearings were too small. Bertness et al. used press perturbations, and did not follow their experiment long enough to observe self-replication of either mussels or *Ascophyllum*.

Bertness et al.’s design violated the “same environment” criterion (Connell and Sousa 1983, Peterson 1984) because their experiment spanned two habitats that show differences in water flow. Their *Ascophyllum* sites were in low-flow areas, and their mussel sites were in high-flow areas. They reported significant differ-

ences in water flow between the two habitat types. Any design that combines sites that differ in water flow into a single analysis does not meet the “same environment” requirement. A valid test of mussel beds and *Ascophyllum* stands as alternative states would have used randomly chosen sites within a single habitat that was as similar as possible with respect to extrinsic environmental variables, such as water motion. Bertness et al. did not do this.

Second, we think that Bertness et al.’s largest patch size (3 × 3 m) was probably too small to detect a switch in *Ascophyllum* stands. We suggested small clearings (≤2-m diameter) in *Ascophyllum* stands would probably revert to *Ascophyllum* and larger clearings (4- and 8-m diameter) may diverge to alternative states that were dominated by mussels or *Fucus* (Dudgeon and Petraitis 2001).

Bertness et al. suggested that their 3 × 3-m clearings in *Ascophyllum* stands are comparable to our 4-m-diameter clearings because they trimmed fronds around the edge so that they would not lie in the plot at low tide. Two points are worth noting. First, consumers forage on a per unit-area basis and so bigger plots experience less foraging pressure per unit area for a given number of consumers. Bertness et al.’s 3 × 3-m clearings, trimmed or not, are only 72% of the area of our 4-m-diameter clearings. Second, we suspect that most of the consumer activity occurs when plots are submerged by the tide and when trimmed fronds would be floating off the surface. Placement of fronds at low tide is unlikely to matter, whereas distance from the floating canopy edge and area of clearing at high tide are likely to be more important.

Third, Bertness et al.’s caging treatment was a press perturbation and so violated the stricture against the use of press perturbations (Connell and Sousa 1983). Connell and Sousa (1983) argued very persuasively that the use of press perturbations, such as caging, are irrelevant for tests of alternative states. Press perturbations also canalize the successional trajectory and reduce the chance of stochastic events, which are crucial to the initiation of alternative states. Thus caging is a test of the ongoing influence of consumers on community structure rather than a test of the switch between alternative states. Indeed, we would suggest that the only observations of interest would be the successional path of the unmanipulated control plots across the different spatial scales of the patch size. Examination of Bertness et al.’s Figs. 6 and 7 suggest succession over three years in the unmanipulated controls was unresolved.

Finally, while Petraitis and Latham (1999) suggested *Ascophyllum* stands and mussel beds in sheltered bays may be alternative stable states, we (Petraitis and Dudgeon 1999, Dudgeon and Petraitis 2001) have been

TABLE 1. Comparison of partly nested designs used in Bertness et al. (2002) and Petraitis and Dudgeon (1999).

Bertness et al. design		Bertness et al. alternative 1			Bertness et al. alternative 2		
Source	df	Source	df	Test denom.	Source	df	Test denom.
Between plots							
Habitats, H	1	Habitats, H	1	H × S	Habitats, H	1	S(H)
		Sites, S	6	no test			
		H × S	6	no test	S(H)	13	no test
Within plots							
Patches, P	2	Patches, P	2	P × S	Patches, P	2	P × S(H)
P × H	2	P × H	2	P × H × S	P × H	2	P × S(H)
		P × S	12	no test			
		P × H × S	12	no test	P × S(H)	26	no test
Within sub-plots							
Caging, C	2	Caging, C	2	C × S	Caging, C	2	C × S(H)
C × H	2	C × H	2	C × H × S	C × H	2	C × S(H)
		C × S	12	no test			
		C × H × S	12	no test	C × S(H)	26	no test
C × P	4	C × P	4	C × P × S	C × P	4	C × P × S(H)
		C × H × P	4	C × H × S × P			
		C × P × S	24	no test	C × H × P	4	C × P × S(H)
Error	117	C × H × S × P	24		C × P × S(H)	52	
Total	134		125			134	

*Notes:* Our design had bays and sites as random, and patch size as fixed. Bertness et al.'s 2002 published design was a three-way factorial ANOVA with habitats, patch size, and caging levels as fixed effects. We assumed their error df = 134 (2 habitats × 8 sites × 3 patch sizes × 3 caging levels minus losses in the one missing mussel site). The two alternatives are partly nested designs. Alternative 1 assumes habitats and sites are crossed with df based on dropping the pair of sites with missing observations. Alternative 2 assumes sites are nested within habitats, and uses all the data (i.e., 8 *Ascophyllum* sites and 7 mussel sites). The column labeled "Test denom." gives the mean square needed to form the correct *F* ratio.

very careful to avoid making statements about the stability based on our experimental results. We think Bertness et al. should be equally cautious in drawing inferences about stability. Their experiment, like ours, was not run for long enough for self-replication of either mussels or *Ascophyllum* to occur.

#### *Pitfalls of partly nested designs and their analysis*

Both Bertness et al.'s (2002) experiment and ours are partly nested designs without replication at the lowest level (Quinn and Keough 2001). Partly nested designs include not only split-plot designs but also univariate repeated-measures designs, and thus these designs can suffer from the well-known difficulties associated with repeated-measures analyses. Bertness et al.'s layout is a classic split-plot design (Cochran and Cox 1967) in which one fixed factor (i.e., caging treatments) is grouped within a second fixed factor (i.e., patches), and they did not analyze their data taking the grouping into consideration. In contrast, our layout and analyses have one random factor (sites) nested within a second random factor (bays). See Table 1 for comparison of designs, degrees of freedom, and format of the analyses.

The correct analysis for Bertness et al.'s experiment would have habitats and sites as main plots, and patch size crossed with caging treatment and both as sub-

plot effects. There are two alternatives for the arrangement of sites and habitats (Table 1). If *Ascophyllum* and mussel sites were, in fact, paired, then sites should be crossed with the fixed treatments of habitat, patch size, and caging. Since one mussel site was lost, the remaining *Ascophyllum* site of that pair should be dropped so the design remains balanced (Quinn and Keough 2001). If sites were not paired, then sites should be nested within habitats.

Bertness et al.'s analyses have "sacrificial" pseudoreplication (sensu Hurlbert 1984, Hurlbert and White 1993) because sources of variation are sacrificed for degrees of freedom. As a result, many of the *F* ratios are incorrectly calculated, and the error degrees of freedom are inflated, which can cause *P* values to be one or more orders of magnitude smaller than the true *P* values (Hurlbert and White 1993). We suspect this is the case in nine of Bertness et al.'s analyses.

Even if Bertness et al. had analyzed their data using split-plot designs, the analyses would have favored finding significant effects for caging and not for patch size. A split-plot layout minimizes spatial variation in environmental characteristics among the sub-plots (i.e., caging treatment levels) compared to the plots (i.e., patch-size treatment levels). As a result, the error estimate associated with the test of the caging effect would tend to be smaller than the error estimate as-

TABLE 1. Extended.

Petraitis and Dudgeon design		
Source	df	Test denom.
Bays, B	3	S(B)
S(B)	8	no test
Patches, P	4	P × B
P × B	12	P × S(B)
P × S(B)	32	

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sociated with the test of the patch size (see Quinn and Keough's [2001] discussion of sphericity in partly nested designs). Thus tests for sub-plots (i.e., Bertness et al.'s consumer effects) would tend to be more powerful than tests of the plot effect (i.e., patch-size effects). Note our partly nested design (e.g., Petraitis and Dudgeon 1999) has the patch-size treatment as part of the sub-plot analysis and so our test of patch size is likely to be more powerful than our test of the effect of bays (see Table 1).

Partly nested designs with the grouping of one factor within another factor can have additional problems with spatial nonindependence (Underwood 1997). It is well known that structures, such as cages, can affect recruitment processes and consumer pressures in "controls" that are in close proximity. Cages may entrain the arrival of larvae not only into caged areas but also onto nearby open areas (e.g., see Kennelly 1991). Caging controls, such as roofs, and the sides of cages themselves, often attract predators and can therefore intensify the effects of consumers on nearby open controls (Underwood 1980, Underwood and Denley 1984; see Menge [1976: Fig. 5] for photographic example). Positive spatial autocorrelation between caged areas and controls may allow true differences to go undetected while negative spatial autocorrelation may allow the converse (A. J. Underwood, *personal communication*).

Bertness et al. do not provide information about the placement of the cage and two controls within a patch. We suspect they must be in close proximity given the sizes of the caging treatments ( $20 \times 20$  cm) and the

patches ( $1 \times 1$  m and  $3 \times 3$  m). If the caging treatments were bunched together then there is the likelihood of spatial autocorrelation. If the cage and the two controls were spread out to reduce spatial autocorrelation then one or more of the caging treatments must have been very close to the edge of the patch.

One could argue that the effects of close proximity of cages and controls are the same over all clearing sizes and habitats and will only add a similar bias to both cage and control. This assumes no spatial autocorrelation, no caging  $\times$  patch size interaction, as well as no interaction of these factors with site. It also assumes effects of caging over time are not multiplicative.

One could also suggest that Bertness et al.'s outcomes for the effects of caging were so highly significant and the effects of patch size were so weakly significant that the results would have been the same even if the analyses were done correctly. We think this would be a misguided interpretation. Smaller  $P$  values for caging effects than for patch-size effects in an incorrectly done analysis do not mean that the effect of consumers is greater than the effect of clearing size, even if the "correct analysis" was done (Underwood and Petraitis 1993). We place the phrase "correct analysis" in quotation marks because even if the analyses were done correctly, they still would not be valid tests of alternative states.

#### *Different ecologies or different ecologists?*

Testing the origin and maintenance of alternative states remains an exciting challenge in ecology, and the notion that similar environments can support alternative community states at different times is controversial to say the least. Clearly some of the difficulty is that protocols for testing the initiation and maintenance of alternative stable states remain misunderstood or improperly applied (Connell and Sousa 1983, Peterson 1984, Sousa and Connell 1985, Petraitis and Latham 1999). It is doubly unfortunate that Bertness et al.'s experiment neither meets the basic requirements for a valid test nor is properly analyzed. Bertness et al.'s (2002) analyses could be redone correctly using partly nested designs, but the experiment would still not be a test of alternative states because of the inclusion of two environments and press manipulations. In addition, any interpretation of a correctly done analysis would be compromised by the possibility of spatial autocorrelation among the caging treatments.

Using identical designs is extremely important if meaningful comparisons are to be made across experiments (Underwood and Petraitis 1993). While Bertness et al. did not replicate our experiment, it is useful to examine two sets of somewhat similar data. Both of us collected data on barnacle recruitment and mussel

mortality. However, they found greater recruitment and mortality than we did. We estimated their average barnacle recruitment densities (from their Fig. 3) to be 220, 200, and 250 barnacles per 100 cm<sup>2</sup> in unmanipulated controls, and in 1 × 1-m and 3 × 3-m clearings, respectively. Our data were 33, 57, 99, 187, 162 barnacles per 100 cm<sup>2</sup> for controls and the 1-, 2-, 4-, and 8-m-diameter clearings, respectively (Dudgeon and Petraitis 2001:Fig. 1).

Bertness et al. found 31.5% and 77.5% mussel mortality in a single tidal cycle (12 h) at the mussel sites and the *Ascophyllum* canopy sites, respectively. All deaths could be attributed to crabs. In contrast, we (Petraitis and Dudgeon 1999) reported very few deaths after 9 days. After 54 days, we found 43% mortality in controls and small clearings (controls and 1 and 2-m-diameter clearings) and 26% mortality in large clearings (4- and 8-m-diameter clearings). We found very few mussels eaten by crabs and 68% of all deaths were due to the predatory gastropod *Nucella lapillus*.

Given the differences in experimental design and sampling protocols, it is impossible to know if differences are due to different ecologies or different ecologists (Underwood and Fairweather 1986). We can only conclude very provisionally that rates of recruitment and mortality differ in nearby regions in the Gulf of Maine.

Finally, it is useful to acknowledge that the world is a more complex and interesting place than one's generalizations. We have never disputed that water motion influences site-specific rates of ecological processes. It is well known that mussels frequently dominate exposed shores or areas of high water motion, whereas *Ascophyllum* often dominates semi-exposed shores (Menge 1976, Lubchenco and Menge 1978, Vadas et al. 1990, Leonard et al. 1998). The interesting question is whether there are places where the outcome is not deterministic and thus alternative states are possible. We believe this may be the case in the sheltered bays, which are a common feature of the coast of the Gulf of Maine. As Lewis (1964:280) noted, without the insights of well-designed experiments, "*Mytilus* appears to stand apart. . . for although it is similarly most numerous on the open coasts but largest in shelter it can also be co-dominant with *Ascophyllum*. . . The possibilities that there are genetic differences, or that there is some special adverse factor on the more sheltered open coasts, are complicated by the erratic distribution of the species on any shore; in neither exposure nor shelter can its presence be foretold with certainty and yet it can be one of the dominant species in either habitat."

#### Acknowledgments

We thank Stu Hurlbert, Mick Keough, Gerry Quinn, and Tony Underwood for their advice on split-plot and partly

nested designs, and Peter Fairweather for his comments on an earlier draft of the manuscript.

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*Ecology*, 85(4), 2004, pp. 1165–1167  
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## ***DO ALTERNATE STABLE COMMUNITY STATES EXIST IN THE GULF OF MAINE ROCKY INTERTIDAL ZONE? REPLY***

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We appreciate the opportunity to reply to Petraitis and Dudgeon (2004)'s comments on our recent paper examining the hypothesis that mussel beds and seaweed canopies on Gulf of Maine rocky shores represent stochastic alternative community states. While they have made some constructive comments, we remain highly confident that in the systems we have studied community recovery from disturbance is highly deterministic and strongly driven by consumer control. In our study, we have asked if mussel bed/seaweed canopy alternative states currently exist in the Gulf of Maine (Bertness et al. 2002, Bertness et al. 2003), while they have simply asked if they are possible (Petraitis and Latham 1999, Petraitis and Dudgeon 1999). These are very different questions, and their criticism of our work fails to recognize this difference. Our experiments have utilized multiple sites (>30 sites) in two different rocky shore environments (open coast and tidal rivers), and the consistency in community recovery in relation to

consumer pressure has been unambiguous. Given the robustness of our results, we will be relatively brief in our response

Petraitis and Dudgeon (hereafter P&D) object to the design of our experiments on the Damariscotta River because physical conditions varied between our mussel bed and algal-canopy sites. However, we attempted to choose mussel bed and algal-canopy sites that were as similar as we could find in terms of physical conditions. We tried to avoid sites with extreme physical conditions to maximize detecting the presence of stochastic alternative states. The mussel bed and algal-canopy sites we chose, however, did indeed differ in abiotic parameters (i.e., flow rates) and that is part of the problem. In the vast majority of habitat in the Damariscotta River, one observes a tight correlation between these two community types and flow rate, and it is this correlation that seems to be the major arbiter of the determinism we have found. We have been unable to find shoreline habitat having strictly identical flow conditions yet with a different community type. Although such places may exist in the Gulf of Maine, we have not observed them. If they do exist, they seem to be remarkably rare.

P&D also argue that we did not use large enough clearings to trigger a state change. It is true that we did not use the largest patch sizes used by P&D, but we did feel that we used a large enough patch size to detect stochasticity in the system. The 9-m<sup>2</sup> patches we used were at the threshold they have previously suggested would lead to stochastic changes. How big is big enough? or perhaps more importantly, How common are 9-m<sup>2</sup> patches (or larger) in the Gulf of Maine? Although ice scour may be important in the northern Gulf of Maine, and more so in the Saint Lawrence seaway and the Canadian Maritimes, its role in central Maine on the open coast seems negligible. Indeed, none of us have observed such large patch formation by any disturbance agent in the more than 20 years that we have been working in the Gulf of Maine. In tidal rivers, patch formation by ice can be important to mussel bed

Manuscript received 22 September 2003; accepted 28 September 2003. Corresponding Editor: S. G. Morgan.

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habitats because ice concentrates as it passes through the constrictions where mussel beds are found. But again patch sizes on the order of 9-m<sup>2</sup> or larger are very rare. The impact of ice on river algal canopies also appears rather negligible when compared to the patch sizes being discussed as part of ecological experiments. Even after the harsh winter last year when much of the northern section of the Damariscotta River was completely frozen, we observed no large patch generation. And when ice does impact algal canopies, it usually does so by giving plants a haircut, leaving the holdfast intact. So while our patches may not have been "large enough," we are left wondering what agents could create patches of such size, and, if they do exist, how important are they on ecological time scales. In the central and southern Gulf of Maine it seems that disturbances of such magnitude are exceedingly uncommon.

Despite the poor dispersal ability of *Ascophyllum*, colonization of large disturbances is not impossible, but can take time. On the Damariscotta River we have documented *Ascophyllum* recruitment to the perimeter of large bare patches and over time (4–5 years) to the center of large disturbances. Even in extremely large disturbances (however rare) such as those used by P&D, we suspect that *Ascophyllum* will eventually colonize them. If this were not the case, it would be difficult to explain why dense *Ascophyllum* canopies dominate low-flow environments in tidal rivers. If large-scale ice scour is important, and *Ascophyllum* was not able to recolonize these disturbances, then these habitats should be mosaics of seaweed canopy, barnacles, and mussels.

P&D argue that our usage of press experiments (caging) in addition to pulse experiments (patch formation) is inappropriate to test for stochastic alternative community states. While this may violate some strict interpretations of theory, we suggest that theory may warrant some reconsideration. By not experimentally examining the role of consumers in these systems, one ignores a fundamental aspect of their natural history. Such criticisms also have rightly been made of experiments examining the link between species diversity and ecosystem function without considering the role of consumers (see Duffy 2002, Paine 2002). That consumers impact community structure in numerous habitat types cannot be disputed, particularly on rocky shores, and to ignore their role in community dynamics during recovery from disturbance will not provide any meaningful insights into how these dynamics unfold.

Our experiments cleared large plots of all space holders and followed recovery in these patches just as P&D have done. In addition to following natural recovery, we followed caged, cage-control, and control plots to assess the impact of consumers on recovery. Our caged

plots accurately forecasted how recovery has progressed in uncaged areas associated with crack-and-crevice refuges from consumers. We acknowledge that cage artifacts can be problematic in some habitats, but strongly defend the prudent use of consumer-exclusion cages as a method to understand the role of consumers in community recovery.

P&D also criticize the statistical analysis of our experiments, stating that we should have used a split-plot or partially nested design. In particular, they suggest that sites should be nested within habitat types and that caging treatments should be grouped within the patch-size treatment. These are fair points, especially concerning the nesting of sites, but we disagree that issues regarding our caging treatments are as black and white as they state. When analyzing the experiment, we reasoned that caging treatments within patch treatments could be viewed as independent because we observed nothing to suggest that there were correlated responses among caging treatments. When placing our cages, we did our best to do so randomly while at the same time trying to make sure that they were not too close to one another or the edge of our patches. In addition, recovery within our plots not associated with our caging treatments was quite heterogeneous, especially in areas having lots of cracks and crevices. Hence, the amount of heterogeneity in recovery outside of caging treatments was much greater and seemed to have little to do with what was occurring inside our caging treatments and open control plots. For these reasons, we considered the caging treatments to be orthogonal.

P&D suggest a split-plot analysis for our experiment and point out that this analysis can also be confounded by autocorrelation problems. Nevertheless, we have re-analyzed our data with the analysis (option 2 in Petraitis and Dudgeon 2004) they suggest. The results of this analysis, despite being more conservative compared to our original analysis, produced remarkably similar results except that patch-size effects and interactions with patch size became more significant for mussel percent cover. Regardless of the analysis used, our results were unambiguous; removing consumers resulted in the rapid recovery of the original community (both mussel beds and algal canopies) within 2–3 years regardless of patch size. We believe in the importance of proper statistics, which is why we have explored P&D's suggestions, but we also think that a sound understanding of the natural history of one's study system is just as important. We will let readers judge our results for themselves.

Perhaps the most important issue in this debate is the question being asked. We have asked explicitly, "Do alternative community states exist in these systems?" This is different than asking "Can they exist?" We suspect that they can, but if they do, they exist in

a very narrow subset of the environments that are typical of rocky shores in the Gulf of Maine. In our numerous collective years of work on tidal rivers and the open coast of the Gulf of Maine, we have failed to observe the presence of mussel beds or *Ascophyllum* canopies that were not tightly correlated with high and low water movement, respectively (Bertness et al. 2002, 2003). Although mussel bed/algal canopy alternative community states are theoretically possible, evidence indicating that they currently exist under the same environmental conditions is entirely lacking. We challenge P&D to provide credible evidence that mussel bed/algal canopy alternative community states are not only theoretically possible, but that they currently exist in the Gulf of Maine under the same environmental conditions. Reference to John Lewis' work is misleading. Lewis (1964) was talking about British shores, not North American shores. On British shores *Ascophyllum* is not the habitat-dominating seaweed it is in New England.

We suggest that a better approach to understanding the *relative* importance of stochastically determined alternative community states is not to demonstrate that they are possible, but to identify the conditions when and where they can occur and *how common they are*. To date, our work suggests that *Ascophyllum*-canopy

and mussel bed communities in the Gulf of Maine are generally deterministic, consumer-driven states, rather than stochastic alternative community states. We suspect that if stochastically determined *Ascophyllum* canopy/mussel bed alternative states exist, they are exceedingly rare.

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